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Spatial shifts in salmonine harvest, harvest rate, and effort by charter boat anglers in Lake Michigan, 1992–2012

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ABSTRACT

Stocked and naturally reproducing salmonids in Lake Michigan support an economically important charter boat fishery which operates from multiple locations around the lake. Charter boat operators depend on the sustainability and spatial availability of salmonid species. We analyzed the spatial distributions of charter boat harvest of brown trout, Chinook salmon, coho salmon, lake trout, and rainbow trout from 1992 to 2012. We found that during this 21 year period fishing effort shifted closer to shore, to the west, and to the north. Harvest of some species, namely lake trout and rainbow trout, shifted towards shallower bottom depths and closer to shore. In contrast, harvests of Chinook and coho salmon have not shifted closer to shore in a consistent manner. We suggest that a variety of factors may have contributed to these trends in harvest patterns, including recent ecosystem shifts in Lake Michigan. While we acknowledge that spatial harvest patterns are unlikely to precisely mirror salmonid distribution patterns, we believe that reporting coarse shifts in harvest has implications for future management options including, but not limited to, stocking decisions and harvest regulations.

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Introduction

Salmon and trout (salmonids) contribute to the economically important recreational fishing industry throughout the Laurentian Great Lakes. In Lake Michigan, harvest of five species of salmonids (brown trout (*Salmo trutta*), Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), lake trout (*Salvelinus namaycush*), and rainbow trout (*Oncorhynchus mykiss*)) by charter boat operators constitutes a large proportion of both harvest (Benjamin and Bence, 2003; Brofka and Dettmers, 2001) and the economic benefit of the fishery (Melstrom and Lupi, 2013). Changes in the spatial distributions of salmonids and the locations of harvest have important implications for individual charter operators, as broad shifts in salmonid spatial distributions and catch rates can threaten the livelihood of local, individual charter operators. At the same time, charter operators are expected to alter where they fish and harvest salmonids in response to shifts in spatial distributions and catch rates. In fact, past studies in various systems have tracked changes in spatial distributions of fishing effort (Swain and Wade, 2003) and harvest (Benjamin and Bence, 2003; Vignaux, 1996)

to infer changes in species distributions, essentially assuming that fishers act as rational agents.

Over the past several decades, the Lake Michigan ecosystem has experienced a large number of biotic and abiotic changes which may influence spatial structuring of biota and ultimately affect distributions of the lake's salmonid top predators and the fisheries that depend on them. Specifically, reduced nutrient loading, various species invasions, and altered climatic conditions may have affected biotic distributions across various spatial axes and scales. Similar to other areas of the Great Lakes (e.g., Lake Superior; Austin and Colman, 2007), Lake Michigan water temperatures have increased in past decades due to warmer air temperatures, resulting in shorter ice coverage (Jensen et al., 2007; McCormick and Fahnenstiel, 1999). Simultaneously, due to aggressive nutrient abatement programs, total loadings of phosphorous to Lake Michigan have generally declined since the early 1970s (Dolan and Chapra, 2012). These physico-chemical changes, coupled with the arrival and expansion of several invasive species, have led to a series of broad-scale biological changes. Perhaps most importantly, the introduction and expansion of dreissenid mussels (first, zebra mussel *Dreissena polymorpha*, now largely replaced by the quagga mussel *Dreissena rostriformis bugensis*) has seemingly contributed to not only an overall decline in seasonal water column primary producers (Pothoven and Fahnenstiel, 2013; Yousef et al., 2014), but also a relative increase in the importance of nearshore production (Fahnenstiel et al., 2010). In addition to a dramatically decreased spring phytoplankton

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bloom (Fahnenstiel et al., 2010; Vanderploeg et al., 2010; Yousef et al., 2014), summer chlorophyll concentrations decreased significantly between 1995–2000 and 2007–2011 (Pothoven and Fahnenstiel, 2013). The potential for dreissenid mussels to contribute to a nearshore shunt in productivity has been highlighted by Hecky et al. (2004). While the extent to which nearshore water column primary production has actually increased over time is unclear, nearshore production appears to have increased relative to offshore production (Brooks and Zastrow, 2002; Fahnenstiel et al., 2010; M. Hutton, Purdue University, personal communication). Moreover, it is apparent that nearshore benthic algal production (especially *Cladophora*) has recently increased (Shuchman et al., 2013), and several studies have highlighted the role of dreissenid mussels in facilitating this increase (Auer et al., 2010; Higgins et al., 2008; Tomlinson et al., 2010).

Not only have physico-chemical conditions and primary production changed in Lake Michigan, but there have also been reported shifts in relative abundances of many consumers and altered trophic interactions. For example, the formerly dominant benthic amphipod, *Diporeia* spp., has declined in abundance by multiple orders of magnitude (Nalepa et al., 2009) and invasive predatory zooplankton (*Bythotrephes longimanus* and *Cercopagis pengoi*) have increased in abundance and become important lake-wide planktivores (Yurista et al., 2010). Historically, invasive alewife (*Alosa pseudoharengus*) have served as both a dominant planktivorous fish in Lake Michigan and the main component of piscivorous salmonid diets (Jacobs et al., 2013; Savitz, 2009; Warner et al., 2008). However, similar to other small-bodied potential prey fish species, such as rainbow smelt (*Osmerus mordax*) and bloater (*Coregonus hoyi*) (Jacobs et al., 2013), alewife biomass in Lake Michigan has generally declined since the 1970s (Tsehaye et al., 2014). An exception to this trend is the nearshore, invasive, benthivorous round goby (*Neogobius melanostomus*), whose abundance has generally increased since arrival in Lake Michigan during the 1990s (Kornis and Vander Zanden, 2010). In turn, some salmonids, especially lake trout, have shifted their diets from consuming primarily alewife to consuming large numbers of round goby throughout the Great Lakes (Dietrich et al., 2006; Jacobs et al., 2010). While this shift in trophic connections is consistent with a system-wide shift towards increased reliance on nearshore and benthic production and decreased reliance on offshore, pelagic production (Rush et al., 2012; Turschak et al., 2014), it is unlikely that all salmonids are equally flexible in their prey consumption patterns. Some salmonid species (i.e., brown trout, lake trout, rainbow trout) display quite varied diets in the Great Lakes (Jacobs et al., 2010; Lantry, 2001; Roseman et al., 2014; Tsehaye et al., 2014) and are likely to consume nearshore fish prey such as round goby (Roseman et al., 2014). Other species (i.e., Chinook and coho salmon) are seemingly less plastic in prey consumption patterns (Savitz, 2009). In fact, Jacobs et al. (2013) demonstrated that the proportion of alewife in Chinook salmon diets in Lake Michigan increased from 1994–1996 to 2009–2010, even though alewife biomass declined during this time period.

Seasonal and inter-annual distributions of these potential prey species could also help to explain spatial trends of salmonid species. Seasonally, various fish species of the Great Lakes, including round goby (Walsh et al., 2007), display shifts to offshore, benthic habitats in the colder winter months. Salmonids may track these forage fishes as they move closer to shore from spring to fall. We are unaware of pronounced, inter-annual shifts in spatial locations of Lake Michigan forage fishes. For example, there has been no obvious shift in depth of capture for alewife in Lake Michigan in recent decades (C. Madenjian, USGS, personal communication). However, annual spatial shifts of forage fishes have been documented in other Laurentian Great Lakes since the arrival of dreissenid mussels (Mills et al., 2003; O’Gorman et al., 2000) and may have occurred in Lake Michigan. Moreover, changes in relative abundance of different forage fishes would lead to spatial changes in overall forage fish biomass.

While spatial shifts in salmonid harvest may partially reflect shifts in salmonid distributions, harvest patterns may also be strongly influenced by variation in catchability, fishing regulations and angler behavior. For example, catchability of fish may respond to ambient water temperature, water clarity, and local foraging opportunities (Danzmann et al., 1991; Gregory and Levings, 1998). In Lake Michigan, angler harvest limits for each salmonid species are related to harvest of other salmonid species, and thus spatial harvest patterns among salmonid species are likely co-dependent. Finally, considerations such as fuel costs and local harvest rates may affect when and where charter boat anglers target salmonids.

Herein, we present an analysis of spatial patterns of salmonid harvests by charter boat fishers in Lake Michigan from 1992 to 2012. Given that the assumption of constant catchability across space and time likely does not hold for charter boat fishers targeting salmonids in Lake Michigan, analysis of charter boat catch data is an imperfect way to assess changes in spatial distributions of salmonids. However, quantifying spatial patterns of salmonid harvest allows us, at a minimum, to assess if spatial trends in harvest patterns are qualitatively consistent with shifts in salmonid distributions expected to have occurred in response to ecosystem level changes. More directly, documenting spatial patterns of harvest may have implications for jurisdiction-specific stocking practices and harvest expectations. To these ends, we analyzed Lake Michigan charter boat harvest data (1992–2012) for trends in mean A) total water column depth, B) distance to shore, C) longitude, and D) latitude of salmonid harvest.

Methods

Charter boat harvest data

We compiled data collected by the Illinois Department of Natural Resources (ILDNR), Michigan Department of Natural Resources (MIDNR), and Wisconsin Department of Natural Resources (WIDNR) that describe charter boat harvest from May to September during 1992–2012 (excluding 1992 for ILDNR). These data describe individual charter boat trips and include the date, number of anglers, hours of effort, number of each species of fish harvested, and location (defined as the 10' × 10' grid cell that was fished; Fig. 1). Each charter captain is required to report these data for each trip, and only one grid cell is reported for each trip. Catch and release data were seldom recorded, especially early in the study period, making it impossible to calculate and use catch rates as estimates of distribution. Information on species targeted during a fishing trip was not consistently recorded. Therefore, to reduce the impact of trips when non-salmonids were targeted, we excluded trips in which ≥20 yellow perch (*Perca flavescens*) were harvested (4299 trips excluded). Most of these excluded trips resulted in the harvest of zero or few salmonids (2567 individual harvested salmonids excluded). When <20 yellow perch were harvested, the rate of salmonid harvest increased to a point where it was appropriate to place a somewhat arbitrary threshold as to not exclude further data. We also omitted trips in which zero total salmonids were harvested because there was no indication of the targeted species; in many of these cases, fishing effort (angler-hours) was low (16,061 trips excluded). Moreover, several of our analytical methods evaluate the spatial location of salmonid harvest and were not affected by trips in which zero salmonids were harvested. Our final data set ($N = 520,441$ trips) consisted of 83,363 trip records from ILDNR, 214,170 trip records from MIDNR, and 222,908 trip records from WIDNR.

Data analysis

Our analysis focused on five salmonid species: brown trout (BNT), Chinook salmon (CHS), coho salmon (COS), lake trout (LAT), and rainbow trout (RBT). To visualize spatial patterns, we calculated harvest per unit effort (HPUE, using angler-hours as the index of

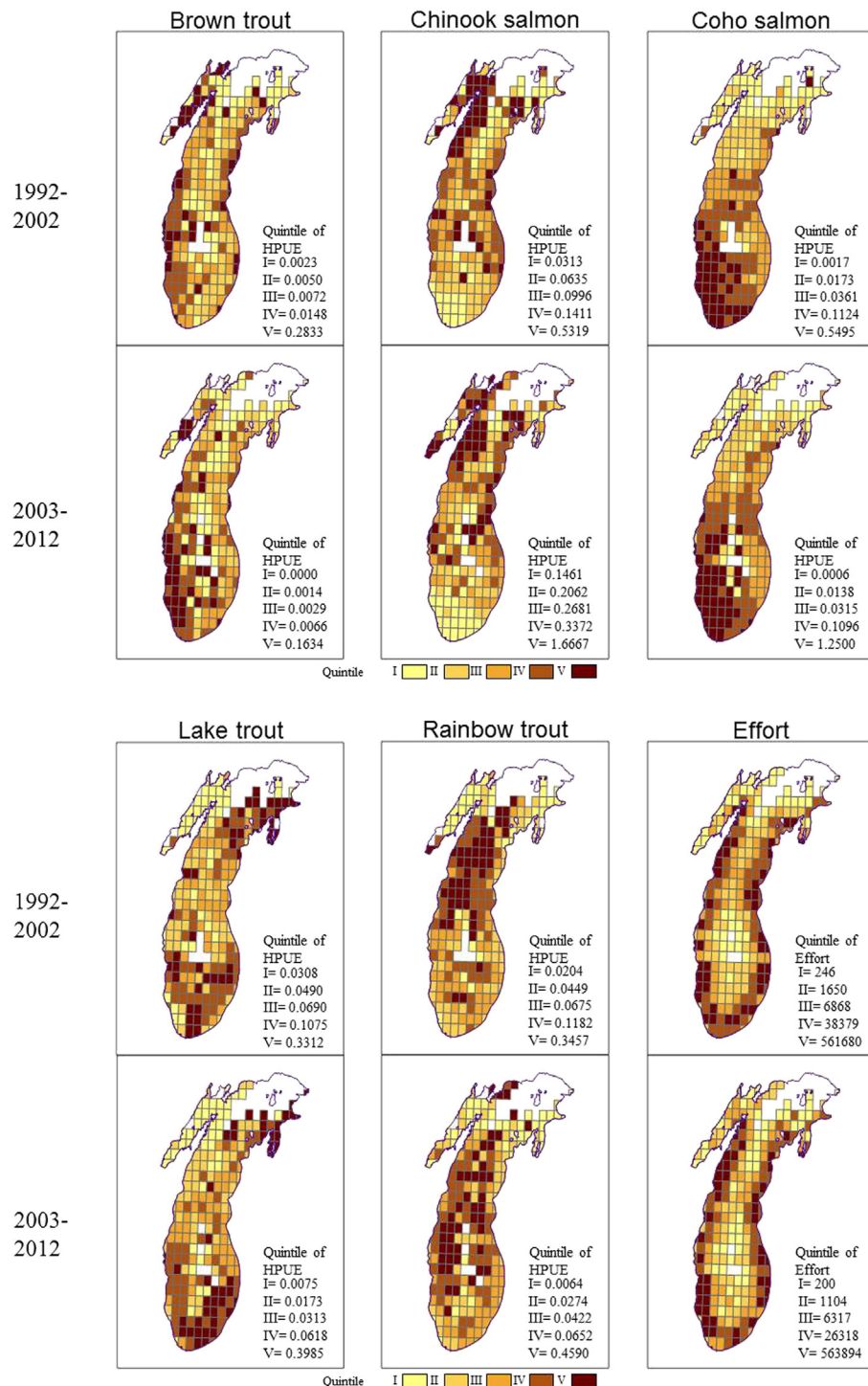


Fig. 1. Quintile maps of harvest per unit effort (fish per angler-hour) and effort (angler-hours) in 10' grid cells. Data are presented for two time periods (1992–2002 on top row and 2003–2012 on bottom row). Provided with each map are the upper cutoff values of each quintile, given by roman numerals I–V.

effort; Höök et al., 2004a, b) of each species in each grid cell within two roughly equivalent time frames, namely, 1992–2002 and 2003–2012. These two time periods also approximate the time period before and after quagga mussel introduction into Lake Michigan. We displayed spatial patterns of HPUE (divided into quintiles) for each time frame using ArcMap (ESRI, 2014). To assess temporal trends, we also regressed this species-specific, lake-wide HPUE, along with total effort and species-specific harvest total, against year (1992–2012).

To evaluate trends in spatial locations of harvest from 1992 to 2012, we calculated mean locations of species-specific harvest across annual and monthly time scales using four location metrics: A) total water column depth, B) distance to shore, C) longitude, and D) latitude. We analyzed trends using data grouped by both year and individual months because past studies of salmonid distributions in Lake Michigan suggest that movement and distributions of salmonids can vary seasonally (Adlerstein et al., 2007a, 2007b, 2008; Höök et al., 2004; Schmalz et al., 2002). We acquired data describing the location (latitude and

longitude) of the centroid and the mean depth (m) of each 10' grid cell. Using these centroid locations, we calculated the shortest distance to shore (m) for each grid cell. To calculate mean locations, we multiplied each of the four location metrics by the number of fish harvested in each grid cell, summed the results for all grid cells, and then divided by the total number of fish harvested from all grid cells across a given time frame (month or year, k),

$$HL_{j,k} = \frac{\sum X_i H_{i,j,k}}{\sum H_{i,j,k}} \quad (1)$$

where HL is the mean harvest location, j is one of the five salmonid species, k is the time scale (either a specific month (e.g., May, June, July) within a given year or a specific year (e.g., 1992, 1993, 1994)), X_i is one of the four location metrics for grid cell i , and H is the number of fish harvested. This allowed us to examine trends across years in species-specific average locations (i.e., trends in mean annual location or location during a particular month over time) as well as trends in species-specific average annual locations across years. To compare coarse differences in spatial patterns between the two time periods (1992–2002 and 2003–2012), we calculated annual HL for each species. We then compared mean HL between the two periods using two-tailed, two sample t -tests assuming unequal variance (year as replicate).

In order to examine temporal trends in the location of harvest, we fit linear regressions to the weighted means (HL s) over time (i.e., from 1992 to 2012) and calculated the associated slopes and 95% confidence intervals for each fit. Given our definition of k and the nature of the dataset (i.e., harvest from May–September for each year), this method resulted in six regressions for each species \times location metric combination: five for monthly average locations (May–Sept.) and one for annual average locations (the sample size for each regression was equal to the number of years considered, i.e., $n = 21$). Regressions for which the 95% confidence interval of the slope did not overlap zero were considered statistically significant trends. We computed all calculations using R version 3.0.3 (R Core Team, 2014).

To coarsely adjust for changes in location of effort over time, we calculated weighted means of angler-hours (number of anglers multiplied by hours of angler effort) for each of the four spatial metrics,

$$EL_k = \frac{\sum X_i E_{i,k}}{\sum E_{i,k}} \quad (2)$$

where EL is a location of effort, E is the number of angler-hours, and k , X_i , and i are as defined above. We then subtracted these weighted mean locations from the weighted mean location of harvest for a given time frame.

$$HL_{j,k} - EL_k \quad (3)$$

where HL , j , k , and EL are as defined above. Effort and harvest means always had the same units (i.e., decimal degrees of harvest minus decimal degrees of effort). Because, in most cases, multiple salmonid species were harvested on a single trip, we used the same effort values across all five species. We again calculated slopes and confidence intervals to examine trends in harvest over time, adjusted for effort.

Given that we combined datasets from three different states and that spatio-temporal patterns may not be equivalent among these states, we performed identical analyses described above for each individual state database (see Appendix A, Figs. S4–S9).

Results

The number of individual fish harvested varied by species, with relatively large numbers of CHS and COS and relatively low numbers of BNT harvested (Fig. 2b). The annual number of CHS harvested

lake-wide increased from 31,304 in 1992 to 215,612 in 2012. CHS was the only species for which annual lake-wide harvest significantly increased from 1992 to 2012 ($r = 0.83$; slope ($\pm 95\%$ CI of slope) = 8928 ± 2667 fish yr^{-1}). Annual lake-wide harvest of BNT ($r = -0.69$; slope = -229 ± 107 fish yr^{-1}), LAT ($r = -0.695$; slope = -1690 ± 786 fish yr^{-1}), and RBT ($r = -0.559$; slope = -767 ± 512 fish yr^{-1}) significantly decreased from 1992 to 2012, while COS harvest did not trend significantly over time ($r = -0.075$; slope = -269 ± 1608 fish yr^{-1} ; Fig. 2b). Similar trends were found in annual lake-wide HPUE from 1992 to 2012 (CHS: $r = 0.857$; slope = 0.013 ± 0.004 fish/angler-hour yr^{-1} ; BNT: $r = -0.788$; slope = -0.0005 ± 0.0002 fish/angler-hour yr^{-1} ; LAT: $r = -0.767$; slope = -0.003 ± 0.001 fish/angler-hour yr^{-1} ; RBT: $r = -0.663$; slope = -0.002 ± 0.001 fish/angler-hour yr^{-1} ; COS: $r = -0.209$; slope = -0.001 ± 0.003 fish/angler-hour yr^{-1} ; Fig. 2c).

Effort and total harvest

Effort significantly increased across the study period from approximately 480,000 angler-hours in 1992 to nearly 700,000 angler-hours in 2012 ($r = 0.617$; slope = 5125 ± 2939 angler-hours yr^{-1} ; Fig. 2a). Effort was generally close to shore (mean distance to shore of effort = 8.73 km; Fig. 1), and shifted closer to shore across the time period studied (Fig. S2b). From 1992 to 2012, effort also shifted to the west (Fig. S2c) and north (Fig. S2d).

The mean spatial locations of total harvest varied among species (Figs. 3–4, S2) and species-specific HPUE varied spatially (Fig. 1). In addition, the five species displayed temporal trends (from 1992 to 2012) in the mean bottom depth, distance to shore, longitude, and latitude of harvest (Figs. S1–S2). These trends were evident even after adjusting for effort (Figs. 3–4). Trends related to the depth or longitude of harvest were not generalizable among species. However, on an annual basis, all species shifted towards being harvested further south (Fig. 3d), and the mean distance to shore of harvest became more similar among species (Figs. S1b, 3b).

Brown trout

Harvest of BNT was relatively close to shore, in relatively shallow water (mean bottom depth of harvest = 40.32 m), and was more common along the western shore (mean longitude of harvest = 87.23° W; Fig. S1). From 1992 to 2012, BNT harvest exhibited two strong spatial trends: one in a southern direction and one in a western direction (Fig. S1). Both of these trends were consistent when calculated on an annual basis and for specific months, and also before and after adjusting for effort (Figs. 4c–d, S2c–d). Distance to shore of BNT harvest increased over time, and this trend became more evident after adjusting for a shift in effort closer to shore (Fig. 4b). Finally, while there were no consistent temporal patterns in the bottom depth where BNT were harvested, there was a marginally significant decrease in mean bottom depth of harvest from 1992–2002 to 2003–2012 ($p = 0.057$; Fig. S3a).

Chinook salmon

From 1992 to 2012, CHS harvest trended closer to shore (Fig. S2b). This trend was evident when harvest data were grouped annually or by individual months. However, relative to effort, CHS harvest shifted further from shore (Figs. 3b, 4b). While other spatial trends of CHS harvest were inconsistent across months, on an annual basis relative to effort, lake-wide CHS harvest shifted further south and to deeper bottom depths (Figs. 3–4, S1–S2).

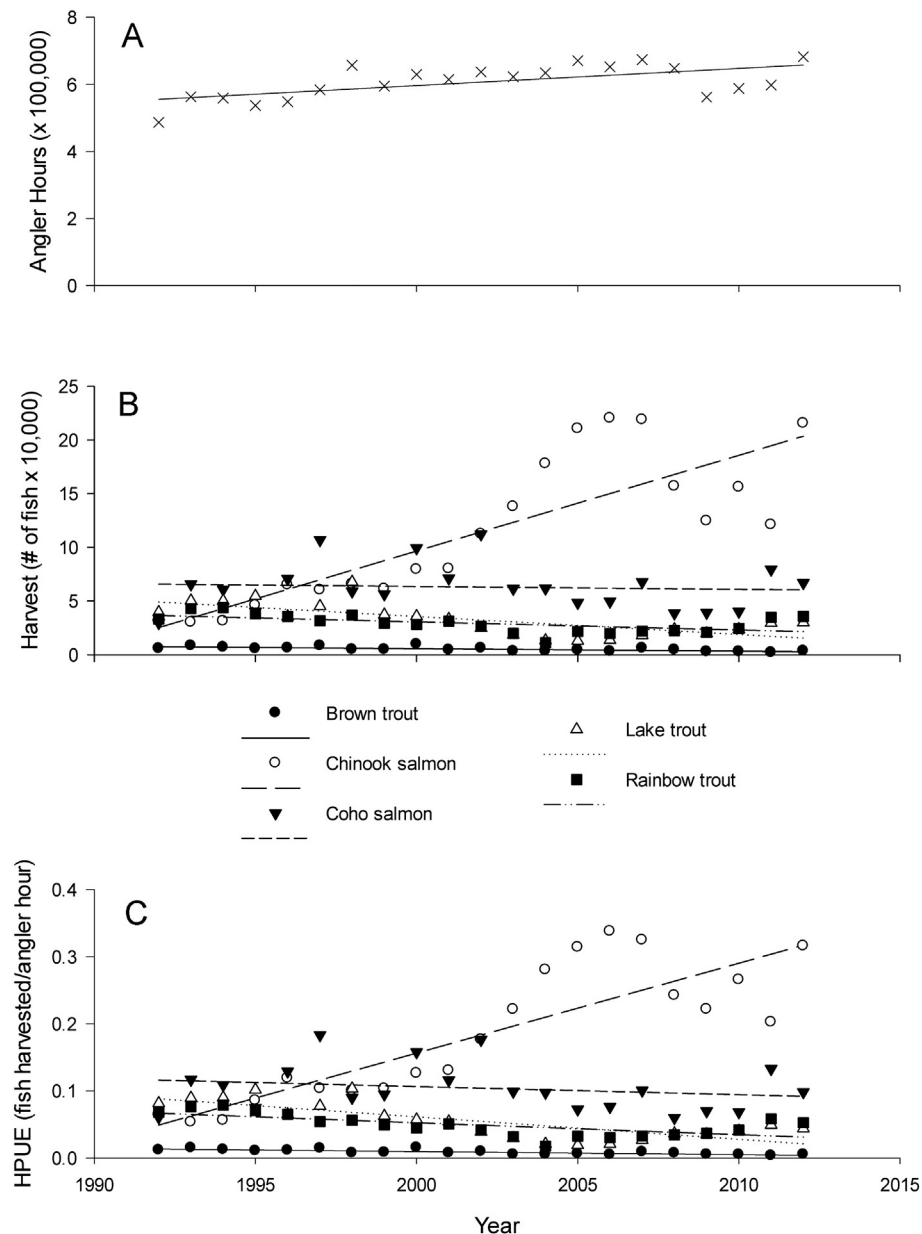


Fig. 2. Temporal trends in lake-wide annual (1992–2012) A) effort (angler-hours), B) species-specific harvest, and C) species-specific harvest per unit effort (HPUE). Data come from information provided by charter boat captains to Illinois, Michigan, and Wisconsin Departments of Natural Resources.

Coho salmon

From 1992 to 2012, COS were more commonly harvested along the western shore (mean longitude of harvest = 87.51° W) and in the southern portion of the lake (mean latitude of harvest = 42.62° N; Fig. S1). The clustering of COS harvest in southwestern Lake Michigan was particularly noteworthy during May–July, whereas during August and September COS harvest along eastern Lake Michigan was relatively high. Temporal trends in location of COS harvest were generally inconsistent across months and differed when adjusting for trends in effort (Figs. 3–4, S1–S2). Moreover, there were no significant changes in location of COS harvest from 1992–2002 to 2003–2012 (Fig. S3). However, August and September harvest (i.e., when COS harvest shifted away from southwestern Lake Michigan) from 1992 to 2012 trended further south and towards shallower bottom depths, and both of these trends were maintained after accounting for location of effort.

Lake trout

Harvest of LAT was more common in the southern portion of the lake (mean latitude of harvest = 43.38° N; Fig. S1). From 1992 to 2012, LAT harvest shifted to shallower bottom depths (Fig. S2a) and closer to shore (Fig. 4b). These trends were consistent both on an annual basis and during most months (Figs. S1a–b, S2a–b), and were evident after adjusting for location of effort (Figs. 3a–b, 4a–b). Finally, LAT harvest shifted eastward over time, which became more evident after adjusting for effort (Figs. 3–4, S1c–S2c).

Rainbow trout

Harvest of RBT displayed two strong spatial trends: one to shallower depths and one closer to shore (Figs. 3, S1). Both trends were consistent when calculated on an annual basis and for most months, and before and after adjusting for effort (Figs. 4a–b, S2a–b). Trends of RBT harvest

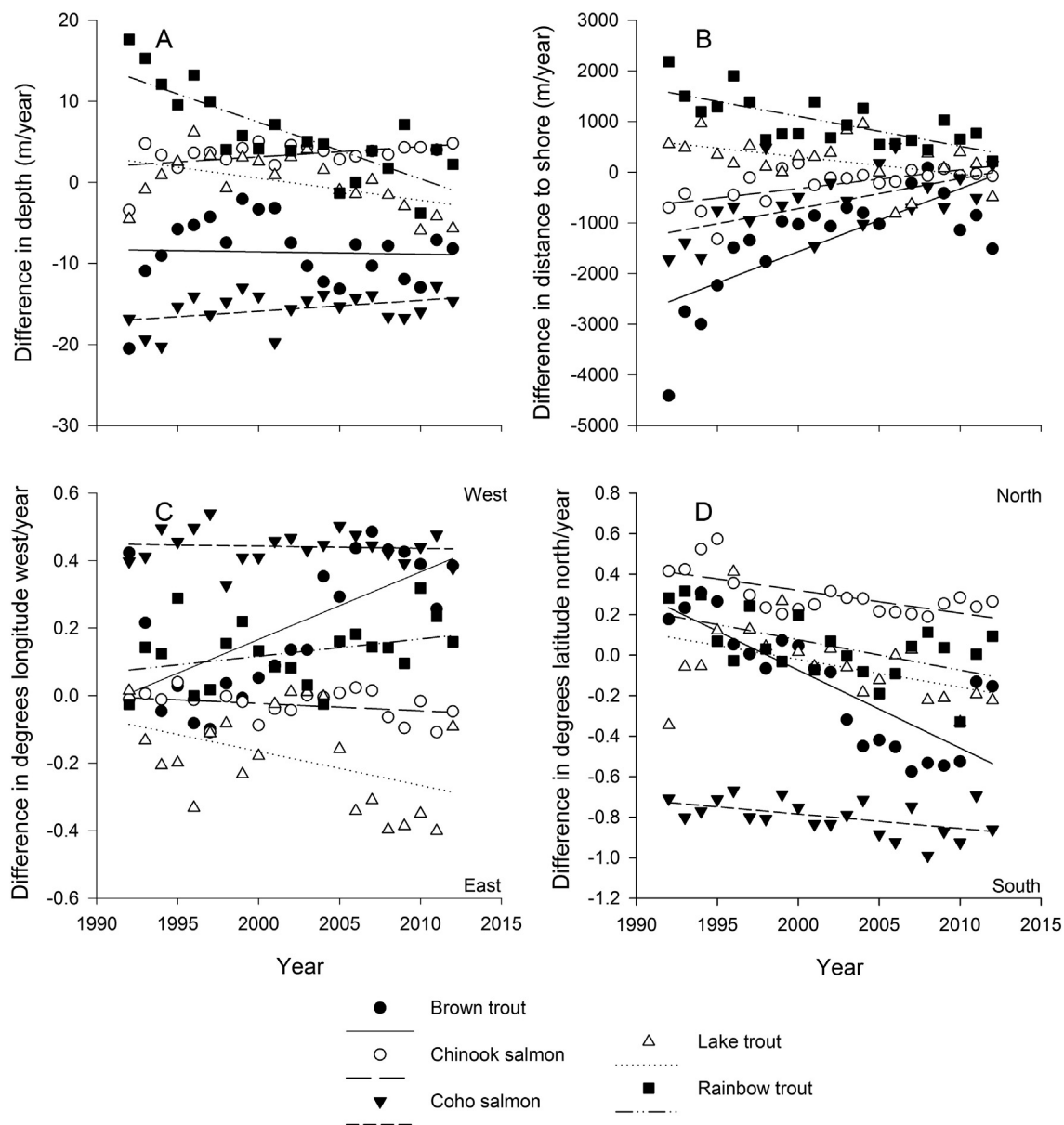


Fig. 3. Regressions depicting temporal trends in lake-wide annual (1992–2012) species-specific weighted averages of harvest after adjusting for effort. A) Depth, B) distance to shore, C) longitude, and D) latitude.

with respect to latitude and longitude were inconsistent across months and after adjusting for effort, but in general RBT harvest shifted towards the south and west (Figs. 3–4, S1–S2).

Discussion

Spatial patterns of salmonid harvest by charter boat anglers in Lake Michigan have shifted over time, which may have important implications for both charter boat operators and agencies involved in the management of this fishery. Due to inconsistencies in catchability, species targeting, and regulations governing harvest of salmonids in Lake Michigan, it is inappropriate to assume that harvest patterns strictly and directly relate to species distributions (see below). However, fisheries researchers have frequently used catch and harvest data to infer species distributions (e.g., Benjamin and Bence, 2003; Swain and Wade, 2003; Vignaux, 1996), and we suggest that it is insightful to evaluate whether harvest patterns are consistent with ecosystem level changes in Lake Michigan and potential responses in species distributions. To this point, spatial patterns of salmonid harvest from 1992 to

2012 are inconsistent with the expectation that salmonids have shifted further north in the lake in response to lake warming. It is also plausible that a variety of factors, including reduced offshore production and nearshore food web changes, have led salmonids to shift closer to shore and/or to shallower bottom depths. While harvest patterns of some species support this possibility, harvest patterns of others do not. Specifically, harvest patterns of LAT and RBT, species which display relatively flexible diets (Roseman et al., 2014; Tsehaye et al., 2014) and tend to be harvested further offshore, have shifted closer to shore and to shallower bottom depths. In contrast, harvest of CHS and COH, species with less flexible diets (high reliance on alewife prey; Savitz, 2009), have not shifted closer to shore and to shallower bottom depths. Finally, the harvest of BNT has shifted westward and further offshore, but not to deeper bottom depths.

There are a number of factors which make it difficult to directly relate harvest patterns to species distributions. Currently in Lake Michigan, there is a daily harvest limit of five combined salmon or trout per person with a minimum length of 25.4 cm per fish. There are two caveats to this regulation: 1) the daily limit of any single species

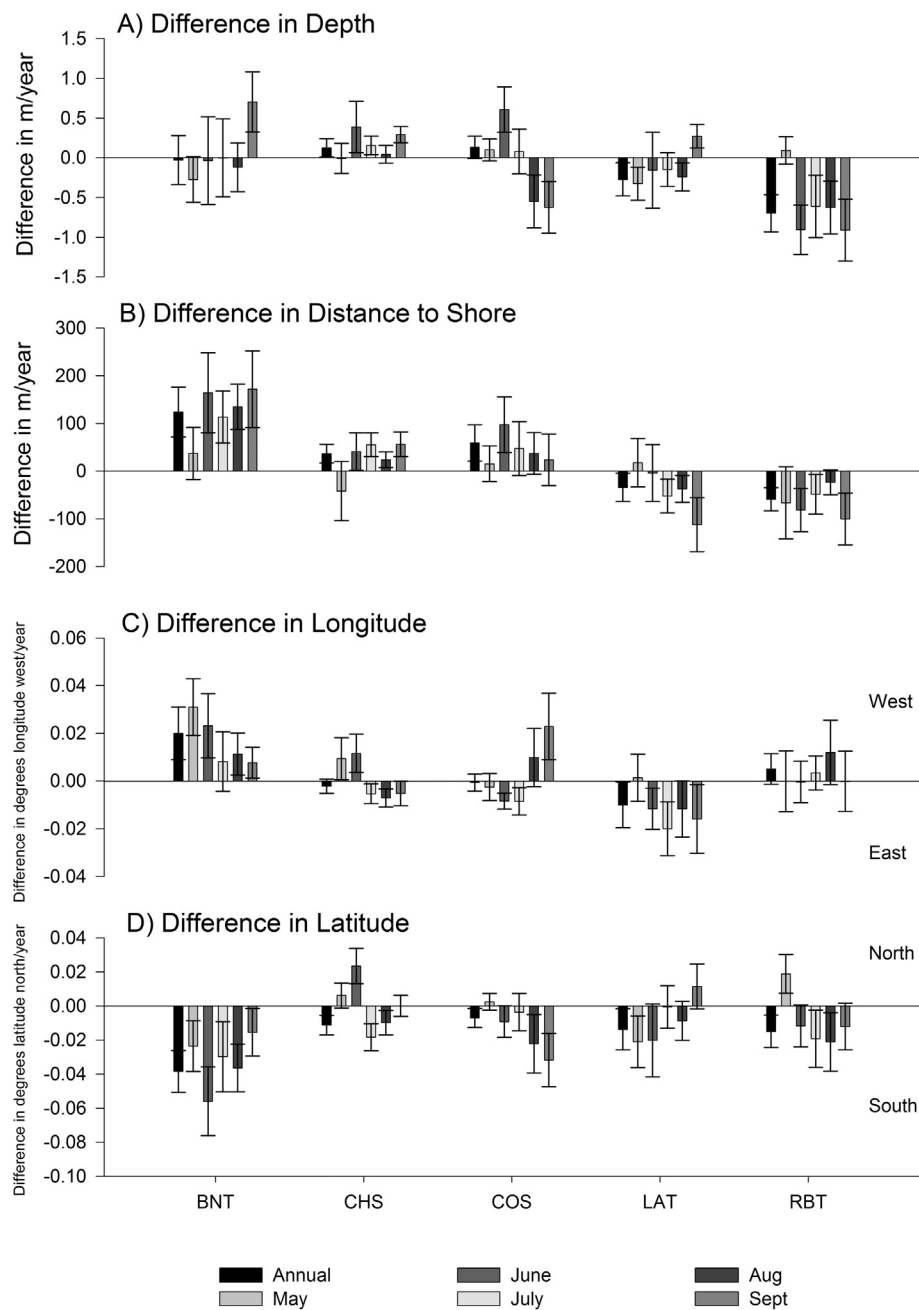


Fig. 4. Regression slopes (with 95% confidence intervals) depicting species-specific trends of annual and monthly weighted averages of harvest after adjusting for effort. A) Depth, B) distance to shore, C) longitude, and D) latitude.

from Michigan waters is three, except for coho and Chinook salmon (five), and 2) the daily limit for lake trout in Illinois and Wisconsin waters is two (Illinois Department of Natural Resources, 2016; Michigan Department of Natural Resources, 2015; Wisconsin Department of Natural Resources, 2015). Regulations have stayed fairly consistent with few changes since 1992 (Trudeau and Hess, 1998). The only major change occurred when Michigan raised the aggregate salmon daily bag limit from three to five in 2010 (Meyerson, 2012). These regulations complicate the interpretation of our results, as harvest of one species may affect the likelihood of another being harvested. Another potential bias involves species targeting by anglers. For the majority of the data considered, the species targeted was not recorded. However, for more recent years (2004–2012), charter operators in Michigan have recorded their original target, although they are often unspecific (e.g., by listing “salmon and trout” as the target). A third potential bias

is non-random placement of effort. Effort shifted closer to shore, to the west, and to the north from 1992 to 2012. Shifts in effort could be reflective of catch success and may also be the result of a combination of socio-economic factors (e.g., charter operators staying closer to shore due to higher fuel prices or to serve more clients in a day, advances in technology and social media allowing charter operators to fish more effectively). These factors could affect the relationship between harvest patterns and species distributions. We attempted to reduce this bias by adjusting for effort in our analysis. Another potential bias involves catchability as a function of environmental conditions. Water clarity in Lake Michigan increased during our study period (Qualls et al., 2007), which may affect the visibility of fishing gear and likelihood of hooking salmonids. Also, alewife densities in Lake Michigan have remained relatively low since 2004 (Madenjian et al., 2012), which may have influenced aggression and willingness to feed and

strike by salmonids. It is also important to note that lake trout stocking has remained fairly consistent since 1985, when a restoration plan was presented for the species (Bronte et al., 2008). The only notable exception has been the addition of deeper strains of lake trout since 2008 (Bronte et al., 2008). Changes in the stocking strategy for any salmonid species may have affected distributions, but the nature and extent of these effects are unknown. Because of these biases, along with several other potential biases not mentioned here, subtle shifts in species distributions may be difficult to detect; however, we suggest that major shifts in species distributions would likely be reflected in harvest patterns.

Although Jensen et al. (2007) and McCormick and Fahnenstiel (1999) showed that Lake Michigan water temperatures have generally increased since 1975, salmonid harvest has not shifted to the north despite a northward shift in effort. Instead, relative to effort, mean harvest shifted south for all five species. A potential reason for this trend is that water temperatures in Lake Michigan may not have reached a temperature warm enough to cause salmonids to shift north. Salmonid species can move vertically in the water column to find their preferred temperature (Levy, 1990). Moreover, while they are cold-water stenotherms, salmonids may be limited by water temperatures in Lake Michigan that are frequently colder than their species-specific thermal preferences (Carter, 2005). In fact, analyses of potential future thermal conditions suggest that warmer temperatures may substantially increase the amount of suitable thermal habitat for salmonids in Lake Michigan (Kao et al., 2014; Magnuson et al., 1990).

It is also plausible that a number of ecological changes would cause salmonids to move closer to shore during the study period. On an annual, lake-wide basis, harvest of four out of the five species shifted closer to shore (BNT was the exception). However, after accounting for the shift in effort closer to shore, only harvest of LAT and RBT trended closer to shore. Additionally, harvest of both of these species shifted towards shallower bottom depths. While LAT in Lake Michigan previously relied heavily on alewife prey (Jacobs et al., 2013; Savitz, 2009), more recent studies of lakes Michigan and Ontario demonstrate a more varied diet, including high consumption of round goby (Dietrich et al., 2006; Jacobs et al., 2010; Turschak and Bootsma, 2015), which is consistent with a shift towards shore and shallower bottom depths. Rainbow trout were caught furthest from shore and thus had the most potential to shift closer to shore and to shallower bottom depths. In addition, RBT have consistently displayed highly variable diets in Lake Michigan, including not only fish prey but also aquatic and terrestrial invertebrates (Jude et al., 1987).

Distance to shore and bottom depth of BNT, CHS, and COH harvest displayed weaker trends, and, relative to effort, harvest of these species generally shifted further from shore. For CHS and COH, these patterns may simply reflect a continued reliance on offshore, pelagic prey such as alewife (Savitz, 2009). The BNT pattern is more perplexing, in part because this species has been reported to display flexible diets (Hyvärinen and Huusko, 2006) and thus we would expect this species to exploit nearshore prey like round goby. Harvest of BNT did display a consistent westward trend, even after adjusting for a westward trend in effort. This strong longitudinal response may reflect more suitable resources for BNT on the relatively rocky west side of Lake Michigan. Moreover, it is interesting to note that from 1992 to 2012, mean harvest locations of all five species shifted towards similar distances from shore (~8 km), and harvest locations of all species have become increasingly similar to the mean distance from shore of effort. However, this concentration of harvest is not evident when considering mean latitude or longitude of harvest, and harvest rates across the five species are highest in different regions of Lake Michigan (see Fig. 1). In other words, we found no evidence that all species have shifted to congregate in a certain area of the lake.

Past studies of salmonid distributions in Lake Michigan and other Great Lakes demonstrate that movements and distributions vary across seasons (e.g., Adlerstein et al., 2007a, 2007b, 2008; Haynes and Keleher, 1986; Höök et al., 2004; Schmalz et al., 2002). While we considered such

seasonal distributions by separately analyzing data across months, changes in the relative abundances of various high-density events could have contributed to spatial harvest patterns over time. For example, salmonids are expected to return to natal or stocking locations to spawn (Patterson and Robillard, 2015; Figs. 4 and S2 suggest this for CHS, COS, and possibly LAT). Therefore, shifts in the dominant sources of natural production of salmonid recruits or changes in stocking locations could have contributed to changes in spatial distributions, in particular during staging prior to spawning.

Documenting shifts in salmonid harvest and potential distributions has a number of possible management implications. Better knowledge of species-specific seasonal spatial distributions could lead to more effective and improved population estimates, a goal of the Wisconsin DNR Lake Michigan management team (Wisconsin Department of Natural Resources, 2013). Moreover, these patterns may have implications for jurisdiction-specific stocking programs, especially if jurisdictions want to maximize the number of stocked fish being harvested in their jurisdiction. Similarly, jurisdictions may adjust fishing regulations to encourage or discourage harvesting of certain species within their jurisdictions.

Many trends of the combined data set were also present in individual state analyses, especially within Michigan and Wisconsin. Trends from Illinois were less consistent, likely due to limited data from this jurisdiction and limited contrast in spatial index values within the relatively small area of Illinois waters of Lake Michigan. Harvest of LAT and RBT displayed consistent trends to shallower bottom depths and closer to shore. Harvest of CHS trended further from shore but not necessarily to deeper bottom depths. Generally, the three states each exhibit a southward trend of harvest of multiple species. These consistent results across smaller spatial scales suggest that the observed patterns are robust to the spatial scale considered. Again, we caution against assuming that shifts in harvest are directly reflective of shifts in distributions of salmonids. However, the magnitude and consistency of some trends suggest that annual and seasonal distributions of salmonids in Lake Michigan have shifted over a 21 year period.

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Appendix A. Supplementary data

Lake-wide trends before adjusting for effort and state-specific trends before and after adjusting for effort.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2016.07.030>.

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